

Observations on the Embryonic Development and Early Post-Embryonic Behavior of *Octopus bimaculatus*

(Mollusca : Cephalopoda)

BY

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(4 Text figures)

INTRODUCTION

Much of the classical cephalopod development research has concerned decapods (see ARNOLD, 1971; ARNOLD & WILLIAMS-ARNOLD, 1977). The first thorough description of octopus development was given by NAEF (1928). At present, development of octopuses has been studied in only a few species. The development of *Octopus vulgaris* (NAEF, 1928; BOLETZKY, 1971), *O. tetricus* (JOLL, 1976; 1978), and *Eledone cirrosa* (MANGOLD, BOLETZKY & FROSCHE, 1971; FUCHS, 1973a; 1973b) has been described in detail. Developmental observations have also been made for *Eledone moschata* (BOLETZKY, 1974), *Hapalochlaena maculosa* (DEW, 1959; TRANTER & AUGUSTINE, 1973), *H. lunulata* (OVERATH & BOLETZKY, 1974), *O. joubini* (BOLETZKY, 1969; BOLETZKY & BOLETZKY, 1969; OPRESKO & THOMAS, 1975), *O. briareus* (BOLETZKY, 1969), *O. cyanea* (DEW, 1959), and *O. dofleini* (GABE, 1975).

Octopus bimaculatus Verrill, 1883 is a common member of the intertidal and subtidal communities of southern California. Female octopuses lay strands of eggs in protected rock shelters and care for the eggs until they hatch. The young are planktonic for 2-3 months (Hochberg, personal communication) before settling to the bottom to assume a benthic existence. This paper describes some of the major aspects of the embryonic development and early post-embryonic behavior of *O. bimaculatus*.

MATERIALS AND METHODS

Research was conducted at the Catalina Marine Science Center on Santa Catalina Island (33°27'N; 118°29'W), 30 km S of Los Angeles, California USA. Between May

1976 and August 1979, 75 brooding octopuses were observed in the field. Regular collections of egg strands from two of these octopuses were used to identify the general course of *Octopus bimaculatus* development. Specific stages of development were investigated by supplemental collections of eggs from other octopuses. After observations and measurements, eggs were preserved in 95% ethanol. In 1978, brooding octopuses were censused approximately weekly to monitor development and determine total length of development (time from first egg laying to first hatching). Because octopuses could not be checked daily, development times are only estimates.

Several octopuses brooded eggs in the laboratory; regular collections were made from one of these. Egg strands from field collections were maintained in the laboratory in containers with a rapid, direct flow of seawater from beneath the eggs. Development proceeded normally in these egg strands for only a few weeks, after which the embryos were no longer viable. Only embryos collected during late stages of development could be maintained until hatching.

The temperature during development was determined by averaging temperature data (recorded at roughly weekly intervals) for the development period. Temperatures in 1977 through 1979 were recorded at the locations where octopuses were brooding. Field water temperatures for 1976 broods (N = 3) were recorded at brooding depth in a similar habitat 1 km away. Since all eggs (laboratory and field) developed at ambient sea temperatures, they were sometimes exposed to short-term temperature fluctuations of several degrees. In addition, all broods were subjected to seasonal warming trends in water temperature, so that temperatures at the end of embryonic development were higher than at the beginning. The effect of

these changes in temperature on timing of development is not known; however, they do represent the natural conditions of octopus development.

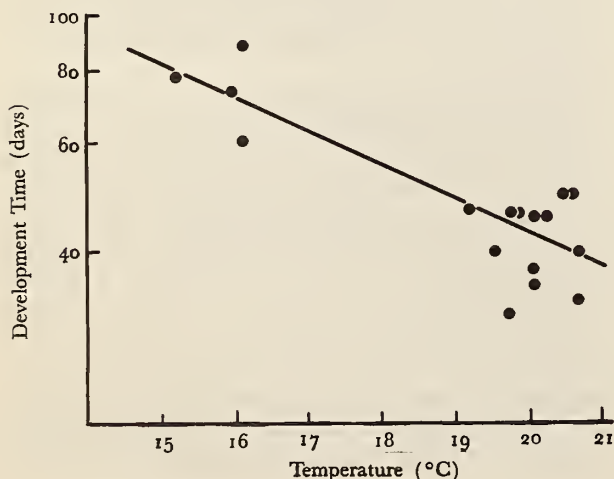
Several juveniles were observed immediately after hatching in the field. All observations were made from 2-3 m to the side of a juvenile to eliminate the effects of turbulence from scuba bubbles.

RESULTS

Octopus bimaculatus females generally lay their eggs over a period of several days. At Catalina, with an average octopus weight of *ca.* 260g, the average clutch size is roughly 20 000 eggs. The number of eggs laid probably varies with the size of the mother; although this relationship was not examined quantitatively, unusually large females appear to have exceptionally large clutches. *Octopus bimaculatus* eggs are twisted into strands of about 100 to 250 eggs each and attached to the substrate. The eggs are ovoid, 3.80 ± 0.24 mm long by 1.34 ± 0.15 mm wide ($\bar{X} \pm SD$, $N = 10$) when laid, with stalks 6 to 7 mm long. Egg size is approximately 5% of the average adult dorsal mantle length (*ca.* 71 mm), and does not appear to vary much, if at all, with the size of the mother.

DEVELOPMENT TIME

Mean estimated development time of *O. bimaculatus* was 50.4 days at a mean water temperature of 19.0°C. The mean water temperature during brooding was 19.7°C for the shortest development time, 31 days, and 16.1°C for



the longest, 90 days. Development time is inversely correlated with water temperature (Figure 1; $r = -0.83$, $p < 0.01$).

EMBRYONIC DEVELOPMENT

The terminology of NAEF (1928) for describing *Octopus vulgaris* embryonic development was found to be suitable for describing the embryonic development of *O. bimacu-*

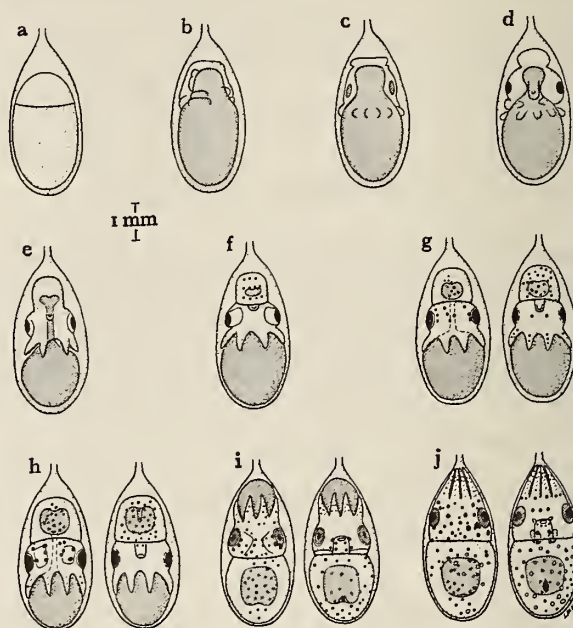


Figure 2

Stages of development of *Octopus bimaculatus*. (a) Stage VI (b) Stage VIII (c) Stage X (d) Stage XI (e) Stage XII (f) Stage XV (g) through (j): dorsal left, ventral right. (g) Stage XVII (h) Stage XVIII (i) Stage XIX (j) Stage XX (Stages after NAEF, 1928; see text for further explanation)

(← adjacent column)

Figure 1

The relationship between temperature and development time in *Octopus bimaculatus*. Development time is the number of days between first laying and first hatching of the eggs, and is plotted on a logarithmic scale; temperature is an estimate of the mean temperature during development. The equation for the line $\ln DT = -0.13(T) + 6.42$; $N = 17$; $r = -0.83$, $p < 0.01$

latus. Representative stages of development are illustrated in Figure 2.

After fertilization, blastodisc development takes place at the free end of the chorion (Stage 1 of Naef). From late stage I to stage VII, the yolk epithelium spreads away from the blastodisc towards the vegetal pole to form a yolk envelope (Figure 2a).

ROTATION AND REVERSAL

The embryos reverse their position in the chorion two times during development. The first reversal occurs at stage VII. Ciliary movement causes rotation of the embryo in a clockwise direction (as viewed from the micropyle, or free, end of the chorion), beginning about stage VIII. The embryo rotates at a rate of 1 rotation/10 minutes at stage X and 16° C. A second reversal at stage XIX returns the *Octopus bimaculatus* embryo to its original orientation within the chorion.

YOLK SACS AND CIRCULATORY SYSTEM

By stage IX, the yolk mass is divided into inner and outer yolk sacs. Pulsation of the outer yolk sac begins at this time and continues through stage XV. The size of the inner yolk sac decreases until stage XV. The inner yolk sac is distinctly bilobed, particularly as it becomes smaller (Figure 2e). At stage XV the inner yolk sac begins increasing in size, and continues to increase until hatching. During this period the size of the outer yolk sac decreases due to transfer of yolk from the outer to inner yolk sacs.

Regular heart beats occur by stage XV. Heart rate increases with advancing development. At 16° C, *Octopus bimaculatus* heart rate increased from 17 beats/min at stage XVIII, to 80 beats/min at stage XIX (stage XIX at 17° C).

ARMS AND SUCKERS

Arm buds first appear at stage IX; the arms are well developed by stage XII (Figure 2e). Three uniserial suckers appear simultaneously at stage XII; a fourth small sucker develops at the tip of the arms by stage XX. Arm movement is frequent at stage XVII, and by stage XVIII the arms move independently of each other and of body movement. At stage XX, the arms may be displaced to one side or near the head rather than neatly encircling the outer yolk sac.

PIGMENTATION

Pigmentation first develops at stage IX, when faint red retinal pigments appear. These pigments darken from tan at stage X to black by stage XIV. Ventral mantle chromatophores develop in the mantle integument at stage XV (Figure 2f; Table 1). Chromatophores on the dorsal surface, which appear in the inner integument closely surrounding the visceral mass, do not develop until stage XVII (Figure 2g). The number of mantle chromatophores, both dorsal and ventral, increases as development proceeds. At late stage XX, many small red chromatophores develop in the outer integument over the dorsal mantle and head.

Head chromatophores develop at stage XVII. Most dorsal head chromatophores develop simultaneously, although 3 additional chromatophores appear around each eye at stage XIX.

Arm chromatophores appear first on the ventral arms, at stage XVII, with chromatophores on the dorsal arms appearing at stage XVIII. Ventral arms have more chromatophores than dorsal arms through most stages, al-

Table 1

Sequence of chromatophore development in *Octopus bimaculatus*

Stage	Body		Head		Arms (per arm)		Funnel
	Ventral	Dorsal	Ventral	Dorsal	Ventral	Dorsal	
XV	10						
XVI	25						
XVII	25	10	2	10-12	2-3		
XVIII	35-40	20	2-4	10-12	3	2 (late)	2 (late)
XIX	40	25	2-4	16-18	4	2-3	4
XX	40-45	25	4-8	16-18	8	8	8

though by late stage XX arm chromatophore distribution is usually more equal.

A pair of funnel chromatophores appear at stage XVIII; by late stage XX there are 8 funnel chromatophores.

There is some individual variation in chromatophore number. Location of chromatophores is also variable; for instance, ventral mantle chromatophores may be neatly aligned in rows in some individuals and randomly scattered over the mantle surface in others.

HATCHING

Octopus juveniles from the same brood hatched over a period of several days. In the laboratory, animals were observed pumping energetically in their egg cases prior to hatching. The egg case usually split near its free end, and the juveniles quickly emerged mantle-first. Agitation of the eggs promoted hatching in both the laboratory and the field. Juveniles which hatch in the field do not have an external yolk sac. Juveniles which were partially raised in the laboratory hatched prematurely. Premature hatching of a given individual was normally completed in 3 to 6 minutes. The external (=outer) yolk sac of premature juveniles occasionally became stuck inside the egg case. In addition to normal mantle contractions and pumping, these juveniles would intermittently lift their bodies up slowly and then drop down, apparently trying to pull loose or "shimmy" out of the egg case. Stuck juveniles would attempt to free themselves for up to 30 minutes, but usually died.

JUVENILE CHARACTERISTICS

Average total length of newly hatched juveniles was 4 mm, with a dorsal mantle length of 2.6 mm and width of 1.5 mm. Arm length was 40% of the mantle length. There were 4 suckers per arm. The newly hatched juvenile chromatophore pattern is shown in Figure 3. The large dorsal body chromatophores lie underneath the mantle and surround the visceral mass; the ventral body chromatophores lie just under the skin covering the mantle.

Within three days after hatching, a few more chromatophores develop, primarily around the eyes and on the web between the arms. Dorsal and ventral head and body chromatophores remain the same as early post-hatching. There are 6-7 suckers per arm, but the suckers near the tips of the arms are not well developed. The weight of 6-day old unfed juveniles was about 1.5-2.0 mg.

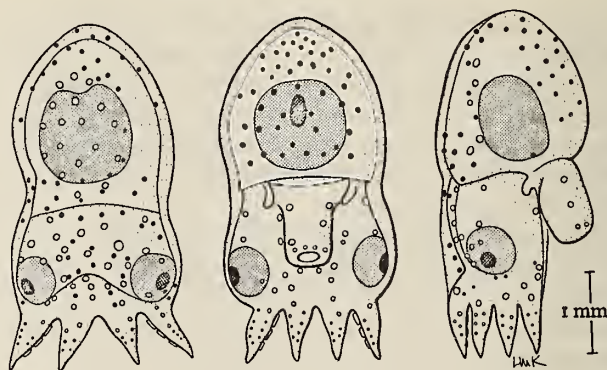


Figure 3

Distribution of chromatophores on newly hatched *Octopus bimaculatus*

POST-HATCHING BEHAVIOR

Newly hatched juveniles of *O. bimaculatus* were planktonic. The juveniles swam both forward (arms-first) and backward (mantle-first), but usually swam backward. Average speed in an observation dish (20 mm diameter), was 1 mm/sec, with frequent bursts of 5 mm/sec. In a 30 cm diameter by 45 cm deep container, juveniles swam somewhat faster but followed the same swimming pattern: slow, regular swimming most of the time, interspersed with rapid bursts of speed covering several centimeters. Juveniles usually swam with chromatophores expanded, but frequently the chromatophores were momentarily contracted. The arms were moved to some extent while swimming.

Although many juveniles swam throughout the entire depth of the container, the majority swam near the bottom, around the edge of the opaque white container; these juveniles repeatedly swam into the wall of the container, rebounded and swam into the wall again. Juveniles accumulated at the lighted region of an otherwise darkened container; they appeared to locate the lighted area by haphazard movements, but remained in the area once it was encountered. When the lighted region was moved, the aggregation of larvae gradually dispersed, then reformed at the newly lighted area.

The swimming behavior of several juveniles which hatched in the field was also observed. All juveniles consistently swam upwards, with their mantles oriented either vertically or at approximately 45°. They did not necessarily swim with the current, even though it was very

strong. Two juveniles were observed for several minutes. The first swam to within 1-2 m of the surface, and was still swimming upwards when observations were terminated. The second juvenile also swam upwards, but nonetheless barely managed to stay at the same depth (5 m below the surface).

Inking was not observed in the laboratory until the juveniles were 4 days old, and even then it only occurred in response to being disturbed. Younger juveniles did not ink, even when handled.

After the contents of a plankton tow were added to the container holding the octopus juveniles, juveniles were occasionally observed to settle on the bottom and nearly double over, reaching under their body with their arms. The function of this behavior is unknown, but it may have been an attempt to remove debris introduced with the tow contents. Several octopuses were observed to attach themselves firmly to the bottom with all arms; one individual moved 1-2 mm along the bottom in this manner, with mantle perpendicular to substrate and arms extended. Small (< 10 mm dorsal mantle length) *Octopus bimaculatus* in the field occasionally exhibit this behavior while confined in a diver's hand.

Three-day old juveniles fed on both laboratory-hatched brine shrimp and natural plankton. One capture was observed: the octopus followed the prey item (probably a calanoid copepod) for several centimeters, swimming arms first, then rushed forward and captured it with its arms. Although a number of juveniles initially fed readily, as evidenced by full guts, later efforts to feed them were unsuccessful.

Four days after hatching in the laboratory, most octopuses were still alive, but were inactive and swam only when disturbed. Most octopuses were dead six days after hatching. The inner yolk sac was noticeably reduced three days after hatching, and completely depleted after six days, so the juveniles probably died of starvation.

DISCUSSION

In 1923, Naef proposed that octopus species with large eggs be included in a separate genus, *Paraoctopus*. PICKFORD & McCONNAUGHEY (1949), working with *Octopus bimaculatus* and *O. bimaculoides*, showed that separate generic status for species with large eggs was not warranted. Rather than simply representing a phylogenetic characteristic, octopus egg size relative to adult size is clearly correlated with mode of juvenile life (BOLETZKY, 1974): octopuses with relatively small eggs have planktonic young, while octopuses with relatively large eggs

have benthic young. *Octopus bimaculatus* egg size is approximately 5% of the average adult dorsal mantle length. As expected on the basis of relative egg size, newly-hatched *O. bimaculatus* juveniles are planktonic. The relative egg size of *O. bimaculatus* is essentially identical to that of *O. rubescens*, *O. salutii*, *O. vulgaris*, and *Eledone cirrosa* (Hochberg, personal communication; OVERATH & BOLETZKY, 1974), and probably to many other species with planktonic young.

The development time of *Octopus bimaculatus* eggs is inversely correlated with water temperature. To explore the generality of the temperature/development time relationship found in *O. bimaculatus*, I have compared information in the literature for other octopus species. Because insufficient data exist at present to evaluate the influence of egg size on development time (although BATHAM, 1957 and MANGOLD *et al.*, 1971 assert its importance), only octopus species with planktonic juveniles (*i.e.*, relatively small eggs) are included. Three species besides *O. bimaculatus* have been studied sufficiently to enable comparison.

The development time of each of the four species is inversely correlated with mean water temperature (Figure 4; *Octopus bimaculatus*: $N = 17$, $r = -0.83$, $p < 0.01$; *O. vulgaris*: $N = 30$, $r = -0.87$, $p < 0.01$; *O. cyanea*: $N = 11$, $r = -0.78$, $p < 0.01$; *O. tetricus*: $N = 7$, $r = -0.87$, $p < 0.01$). There is considerable variability in development time within each species, up to 20 days at the same temperature; over a short temperature range this variation could mask an overall trend. Nonetheless, the significant and consistent trend over a total range of 17°C suggests that this relationship is generally true. Although the \ln development time/temperature relationship appears essentially linear, at temperature extremes there are marked non-linearities. The decelerating rate of development at low temperatures suggests the presence of a minimum temperature below which development will not take place.

The inverse correlation between development time and water temperature has previously been suggested for *O. vulgaris* by MANGOLD-WIRZ (1963) and MANGOLD & BOLETZKY (1973). The analysis presented here corroborates the existence of such a relationship in *O. vulgaris* and suggests that it exists for octopuses in general. OPRESKO & THOMAS (1975) state that there is no apparent correlation between temperature and development time in *O. joubini*. However, analysis of the relationship between average temperature and development time (data from table 2 of OPRESKO & THOMAS) indicates that, in spite of a temperature range of only 1.9°C, there is a significant negative correlation ($N = 10$, $r = -0.64$, $p < 0.05$).

Some species-specific differences in development time are expected as a result of differences in the length of time

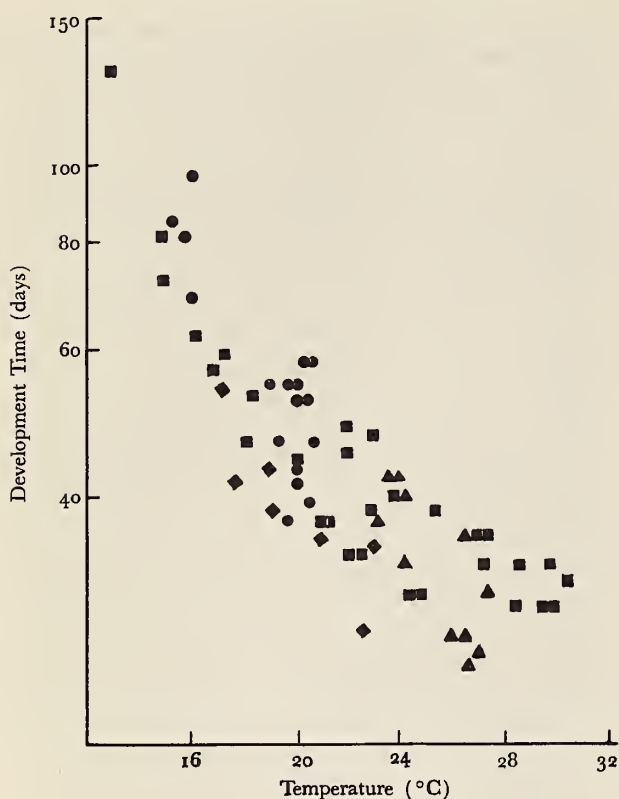


Figure 4

The relationship between temperature and development time in octopuses with planktonic young. Development time is plotted on a logarithmic scale

- - *Octopus bimaculatus* (this paper)
- - *Octopus vulgaris* (MANGOLD-WIRZ, 1963; WODINSKY, 1972; MANGOLD & BOLETZKY, 1973)
- ▲ - *Octopus cyanea* (VAN HEUKELEM, 1973)
- ◆ - *Octopus tetricus* (JOLL, 1976; 1978)

spent in the plankton, environment inhabited, etc. Differences between species would also be expected if the amount of yolk (*i. e.*, egg size) were more important than temperature in determining development time (MANGOLD *et al.*, 1971). The data for the four species examined in Figure 4 appear to fit a single \ln development time/temperature relationship. (The equation for that line is $\ln DT = -0.07 (T) + 5.21$; $N = 65$, $r = 0.84$, $p < 0.01$.) Small sample sizes, large intraspecific variability, and dissimilar investigative techniques make comparisons between species imprecise. However, examining the differences between *Octopus bimaculatus* and *O. tetricus* shows that in spite of a larger egg size (3.8 mm for *O. bimacu-*

latus, 2.4 mm for *O. tetricus*) several clutches of *O. bimaculatus* developed very close to the mean development time and temperature for *O. tetricus*. There may be no actual differences between the 4 species, or perhaps differences are slight because all have relatively small eggs. In any case, there is not enough information to distinguish species-specific differences at this time, and future work here is clearly indicated.

The inverse correlation between development time and temperature may explain in part the seasonal migrations into shallow water for breeding which have been reported for a number of octopus species (*O. vulgaris*, MANGOLD-WIRZ, 1963; *O. defilippi*, VÉRANY, 1851; MARGHAND, 1907; *O. dofleini*, MOTTET, 1975; *O. rubescens*, Hochberg, personal communication). Since shallow water is almost invariably warmer than deep water, migration to shallow water to breed will reduce development time. Shorter development time could reduce mortality by exposing the brooding female and her eggs to predators for a shorter period of time.

The embryonic development of *Octopus bimaculatus* closely resembles that of *O. vulgaris* (NAEF, 1928) and *O. tetricus* (JOLL, 1978). The development pattern of major embryonic features is nearly identical for the 3 species, with differences resulting primarily from small shifts in timing. For example, *O. bimaculatus* undergoes its second reversal at stage XIX, rather than stage XVII as in *O. vulgaris* and *O. tetricus*.

The most notable difference in development among these 3 species occurs in pigmentation. FIORONI (1965) has documented chromatophore development in *O. vulgaris* in detail, thus allowing comparison with *O. bimaculatus*. In *O. vulgaris*, ventral body chromatophore number increases rapidly to 15 chromatophores at stage XVI, then gradually increases to 20 chromatophores at stage XX. In contrast, *O. bimaculatus* ventral body chromatophore number increases very rapidly to about 40 chromatophores at stage XVIII and stops. Dorsal body chromatophores appear later in *O. bimaculatus* and increase to a greater number. Finally, dorsal head chromatophore development is nearly simultaneous in *O. bimaculatus*, rather than sequential as in *O. tetricus* (JOLL, 1978) and *O. vulgaris*.

A comparison of morphometrics of newly hatched juveniles for 9 species of octopods with planktonic juveniles (Table 2) reveals a wide range of sizes, from 2.5 mm to 7.0 mm in total length. There is also considerable variation in the number of suckers per arm (3 to 14), which may be inversely correlated with the length of time the juveniles spend in the plankton, since benthic juveniles hatch with many more suckers per arm (*O. joubini*, 26, and *O.*

Table 2

Morphometrics of newly hatched planktonic juveniles

Species	Total length (mm)	Mantle length (mm)	Mantle length (% adult ML)	Arm length (% ML)	Number of suckers per arm	Reference
<i>O. tetricus</i>	2.5	1.5 ¹	—	50 ¹	3	JOLL, 1976, 1978
<i>O. vulgaris</i>	3.0	2.0	2	35	3	BOLETZKY, 1969, 1977; OPRESKO & THOMAS, 1975
<i>H. lunulata</i>	—	2.3	4	50	10	OVERATH & BOLETZKY, 1974
<i>R. australis</i>	3.7	2.4 ¹	—	43	4	BROUGH, 1965
<i>O. bimaculatus</i>	4.0	2.6	5	40	4	This paper
<i>O. dofleini</i>	—	3.5	—	50	11-14	GABE, 1975
<i>O. salutii</i>	—	3.5	3.5	—	4	BOLETZKY, 1977
<i>O. maorum</i>	7.0	4.5 ¹	—	50 ¹	7-8	BATHAM, 1957
<i>E. cirrosa</i>	—	4.5	3.5	50	8	MANGOLD <i>et al.</i> , 1971

¹measured from figure

briareus, 35, MANGOLD *et al.*, 1971; *H. maculosa*, 20, OVERATH & BOLETZKY, 1974). The similarity in relative arm length, pointed out previously by OVERATH & BOLETZKY (1974), may also be related to a planktonic existence, since benthic juveniles have relatively longer arms (100-160% of dorsal mantle length, MANGOLD *et al.*, 1971; OVERATH & BOLETZKY, 1974). The presence of long arms at hatching may be an adaptation to an immediately benthic mode of life; while the arms and suckers of planktonic juveniles are suitable for holding onto floating objects (JOLL, 1978), they would not be adequate for extensive crawling on the bottom (BOLETZKY, 1977). In *O. bimaculatus* juveniles, attachment to the bottom seemed to be a response to disturbance, and the short movement of one juvenile was definitely not normal crawling behavior.

The distribution of chromatophores on newly hatched juveniles varies considerably from species to species. Chromatophore patterns present at hatching are generally related to the habit of the newly hatched young (WELLS & WELLS, 1977). For instance, *Octopus briareus* young, which are benthic, hatch with a well developed and dense assemblage of chromatophores (WOLTERDING, 1971), while *O. bimaculatus* juveniles hatch with fewer chromatophores. BOLETZKY (1977) suggests that the number of chromatophores is merely related to body size rather than post hatching mode of life. However, a comparison of species with newly hatched octopuses of the same size, such as *Hapalochlaena maculosa* (figure 7 of TRANTER & AUGUSTINE, 1973) and *O. maorum* (figures 1 and 2 of BATHAM, 1957), indicates that the planktonic juveniles have fewer chromatophores.

There are also distinct if less dramatic differences in chromatophore patterns among species with planktonic

young. *Octopus bimaculatus* has fewer dorsal body and arm chromatophores than *O. maorum* (BATHAM, 1957) but more than *O. tetricus* (JOLL, 1976) and *O. vulgaris* (FIORONI, 1965), as might be expected on the basis of size (Table 2). However, in spite of its intermediate size *O. bimaculatus* has a great many more ventral mantle chromatophores than *O. tetricus*, *O. vulgaris* or *O. maorum*. Presumably, the dissimilar chromatophore patterns have an adaptive value, perhaps relating to dissimilar conditions in the plankton experienced by the various species.

The continuous upward swimming of *Octopus bimaculatus* juveniles immediately after hatching in the field is consistent with the positive phototaxis exhibited in the laboratory. This behavior, which apparently has not been reported for other octopus species, would ensure that the young maintain an appropriate position in the water column while planktonic.

SUMMARY

The development time of *Octopus bimaculatus* is inversely correlated with water temperature. Comparison with data for 3 other species of *Octopus* with planktonic young indicates that the development times of all 4 species exhibit a similar response to temperature.

The embryonic development of *Octopus bimaculatus* closely resembles that of other octopus species with planktonic young. The development patterns of major embryonic features are nearly identical to that of *O. vulgaris* and *O. tetricus*, with differences resulting primarily from small shifts in timing. The most noticeable differences in development occur with respect to pigmentation, in both num-

ber of chromatophores and the sequence of their development.

Octopus bimaculatus juveniles from the same brood hatched over a period of several days. The newly hatched young were planktonic. The typical juvenile swimming pattern in the laboratory involved slow, regular swimming interspersed with rapid bursts of speed covering several centimeters, although juveniles in the field seemed to swim at a constant speed. In the laboratory, juveniles exhibited positive phototaxis. Some 3-day old juveniles fed on brine shrimp and natural plankton. Nevertheless, most laboratory-reared juveniles were dead 6 days after hatching, probably from starvation.

ACKNOWLEDGMENTS

I thank B. Nelson, G. Hageman, F. G. Hochberg and K. Mangold for comments on earlier drafts. F. G. Hochberg generously provided unpublished data. J. A. Coyer provided the water temperature data for 1976. This paper is contribution No. 49 from the Catalina Marine Science Center.

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